THE MORPHOLOGY AND SYSTEMATIC POSITION OF THE ALEPOCEPHALOID FISHES

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INTRODUCTION

THE alepocephaloids are black, marine fishes living today in fairly deep to very deep water. Their maxillary is included in the gape, and they have no gas bladder and no adipose fin.

The group has received some, though by no means adequate, taxonomic attention in recent years. Parr (1951, 1952) provided preliminary accounts of the Alepocephalidae and in 1960 reviewed the related Searsidae (or Searsiidae ; Parr's spelling of the family name will be used here). Marshall (1966) described the new family Bathyprionidae, and, on the basis of previous accounts, removed *Leptochilichthys* from the Alepocephalidae and erected a separate family, Leptochilichthyidae, for it. Most recently, Nielsen & Larsen (1968) have shown that the controversial Bathylaconidae (Parr, 1948) belongs with the alepocephaloid fishes.

Though the above five families appear to form a coherent, if varied, group of related fishes, their position in the Teleostei has remained obscure. Usually they have been treated as dubious relatives of the clupeoid or salmonoid fishes, but sometimes as a separate group, e.g., Marshall (1966). The basic difficulty has been a lack of knowledge concerning the internal structure of alepocephaloids. The most complete account of the osteology of the head remains that of Gegenbaur (1878) for *Alepocephalus rostratus*. Derschied (1924) described the nasal apparatus of the same species. Parr (1960) noted certain superficial head bones in some searsids. Gosline (1960) and Patterson (1968) have discussed and illustrated the caudal skeleton of *Alepocephalus rostratus* and Bonde (in Nielsen & Larsen, 1968) figured that of *Bathylaco nigricans*. Two illustrations of the head skeleton of *Bathyprion danae* by Bertelsen and a description and figure of some of the visceral organs of the same fish have been published by Marshall (1966). Nelson (1967), in a paper on epibranchial organs, has provided a figure of the posterior gill arch structure of *Alepocephalus macropterus*. McAllister (1968) summarized data on the branchiostegal rays of alepocephaloids. Greenwood et al. (1966 : 373, 374) have reviewed most of what is known about the osteology of the group, adding certain items of information not to be found elsewhere.

In the present paper the osteology of *Alepocephalus rostratus* (Fig. 1) will be treated in detail. Though this species is probably a rather specialized alepocephaloid, it is the only one for which a specimen was available for staining and complete dissection. Comparative material used to a more limited extent included two skeletons of *A. rostratus* and preserved specimens of the alepocephalid *Xenodermichthys socialis* and the searsid *Searsia koefoedi* in the British Museum (Natural History) ; preserved specimens of the bathyprionid *Bathyprion danae* and the bathylaconid *Bathylaco nigricans* in the Zoological Museum in Copenhagen ; and a preserved *Alepocephalus macrocephalus* at the University of Hawaii.
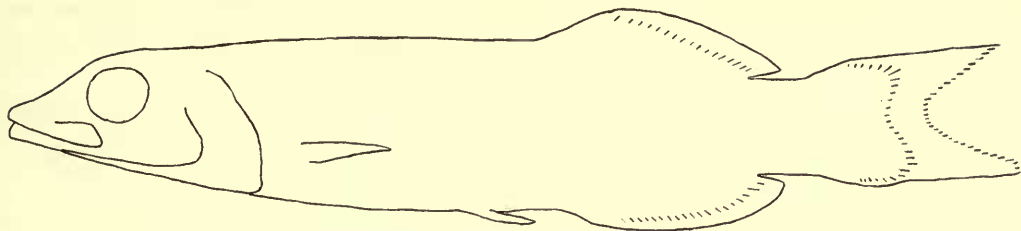
FIG. 1. Sketch of *Alepocephalus rostratus*, based on the
350 mm. specimen dissected.

MATERIALS AND METHODS

A single specimen of *A. rostratus*, 350 mm. in standard length, taken off the coast of Ireland (52° 06′ N 12° 27′ W) in about 380–455 fthms of water by Mr. A. Wheeler in July, 1968 was dissected. This specimen is part of the British Museum (Natural History) collections. The specimen was preserved in formaldehyde, and transferred to alcohol. For one day during the time it was soaking in water prior to placement in alcohol, a slight amount of potassium hydroxide and considerable alizarin solution was added to the water. This had the effect of staining all the superficial bones a dark red, the deeper bone pink, and some of the bony elements most deeply embedded in flesh, e.g., the intermuscular bones, not at all.

There are certain advantages and disadvantages to this method of preparation. In the first place, with a skeleton as largely cartilaginous as that of *Alepocephalus*, a dried skeleton shrivels considerably. As compared to a clearing and staining technique, the method used here (assuming that the fish had been left in stain longer and that the stain had penetrated better) has advantages and disadvantages. In the first place, there is perhaps some question whether a fish of 350 mm. could be adequately and feasibly cleared. Second, the specimen used here is far easier to work with than one in glycerin. During dissection it was merely covered with a wet rag (though this did not altogether prevent shrinking of the cartilage). Third, the muscles and their attachments and, to some extent, the lateral line canals were easier to see than if the specimen had been cleared. The great disadvantage of the present technique lies in the fact that in the vertebral column and related bones, each item, e.g., intermuscular bone, has to be dissected individually. This is not only tedious, but there is always the possibility of losing elements during dissection. For the determination of ribs and intermuscular bones and their relationships a cleared and stained specimen is far better.

ABBREVIATIONS USED IN FIGURES

Ac	actinost		bl	Baudelot's ligament
ah	articular head		Bo	basioccipital
Al	autopalatine		Br	branchiostegal ray
An	angular			
Ao	antorbital		ca	cartilage
Ap	autopterotic		Cb	ceratobranchial
Ar	articular		Cl	cleithrum
As	autosphenotic		cn	cartilaginous nodule

Co	coracoid	mp	superficial epaxial musculature to post-temporal
De	dentary	Ms	mesopterygoid
Dl	dermopalatine	Mt	metapterygoid
Dp	dermopterotic	mu	median band of musculature to supra-occipital
Dr	dorsal ray		
Ds	dermosphenotic	Mx	maxillary
Eb	epibranchial	Na	neural arch
Ec	ectopterygoid	Ns	neural spine
El	epipleural		
em	epaxial musculature	Op	opercle
En	epineural	or	orbit
Ep	epiotic		
Es	extrascapular bone	Pa	parietal
Et	ethmoid bone	Pd	predorsal bone and cartilage
Ex	exoccipital	Pe	uppermost pectoral ray
		Pl	pleural rib
Fr	frontal	Pm	premaxillary
		Po	posttemporal
gr	groove for attachment of the adductor hyomandibulae	Pp	preopercle
		Pr	prootic
		Ps	parasphenoid
hm	hypaxial musculature	Qu	quadrate
hs	socket for hyomandibular articulation		
Hy	hyomandibular	Ra	radial
		Sa	sesamoid articular
Ib	infrapharyngobranchial	Sb	suprapharyngobranchial
Io	interopercle	Sc	scapula
		Sl	supracleithrum
Le	lateral ethmoid	So	supraorbital
li	ligament	Sp	subopercle
Ll	lateral line ossicle	ss	suspensorium
ll	lateral line to body	Su	supraoccipital
lp	ligament to posttemporal	Sy	symplectic
ma	lateral epaxial muscle to autopterotic	tf	lateral exit of trigemino-facialis nerve complex
mc	Meckel's cartilage		
me	deeper epaxial musculature to epiotic, etc.	va	exit for vagus nerve
Mo	mesocoracoid	Vc	vertebral centrum

THE OSTEOLOGY OF ALEPOCEPHALOID FISHES WITH PARTICULAR
REFERENCE TO *ALEPOCEPHALUS ROSTRATUS*

Bone formation

Alepocephalus rostratus is weakly calcified. The dermal bones of the head, which stain the most deeply in alizarin, are thin sheets easily stripped off from the underlying chondrocranium (Gegenbaur, 1878). In the skull much cartilage is retained. At least in the front of the vertebral column the centra do not appear to be ossified; nevertheless, the fact that their identity remains in a dried skeleton suggests that

they are fibrous rather than cartilaginous.   The endochondral bones of the skull are opaque, like the cartilage, and take up very little alizarin.   As Gegenbaur (1878) pointed out, the endochondral bones show concentric markings, suggesting growth rings.   However, in the 350 mm. specimen of *A. rostratus* most of the endochondral bones remain separated from one another by cartilage.

The dermal bones, as suggested, are fragile and easily fractured.   Such fracturing apparently occurs frequently in life.   The extent of dermal ossification also seems to vary considerably among species of alepocephaloids.   Thus, in *A. rostratus* the lateral ethmoid is a small, completely endochondral bone completely surrounded by cartilage (Fig. 4,Le), but in some searsids it forms a significant portion of the skull roof (see Parr, 1960) and is probably capped by dermal bone.   Again, the circum-orbital bones, aside from the lacrimal, may be reduced to tubular ossicles, as in *A. rostratus*, or expanded into plates in some searsids.

It may well be that the unusually poor calcification of the *Alepocephalus* skeleton serves as a partial density compensation for the lack of a gas bladder (Denton & Marshall, 1958).   In any event, the dried skeletons of *Alepocephalus rostratus* are very light in weight.

The sensory systems and associated ossifications

Alepocephalus rostratus has a very large eye (Fig. 1) and a well-developed olfactory rosette ; on the other hand the lateral line canals of the head, particularly on the dorsal surface of the head, are fragmented, reduced in size, and apparently without open pores.   However, in such a fish as *Bathyprion danae* (Marshall, 1966, fig. 1) the eyes are small, and in *Searsia koefoedi* the lateralis system of the head is expanded as a series of arborescent tubules, each ending in an open pore.   Thus the alepo-cephaloids as a whole can hardly be characterized in terms of any particular sensory development.

The olfactory apparatus.   The nasal apparatus of *Alepocephalus rostratus* has been described and figured by Derschied (1923, pp. 115–118, fig. 11).   The anterior and, especially, the posterior nostrils are ample holes without bordering collars separated by a bridge of skin.   These lead into a large, simple nasal cavity most of which lies anteroventral to the nasal openings.   In the posterodorsal portion of this cavity and below the nasal openings lies a typical but well-developed nasal rosette.

The antorbital-supraorbital strut, used by so many isospondylous fishes as a method for pumping water in and out of the nasal cavities and hence across the nasal epithelium (Derschied, 1923 ; Gosline, 1961 ; Kirkhoff, 1958) does not occur in *Alepocephalus rostratus*.   There is no supraorbital bone in this fish, and the ant-orbital is a weak L-shaped splint lying free in the skin.   (In *A. macropterus* both the supraorbital and antorbital bones are absent.)   Nevertheless, it seems probable that the nasal sac of *Alepocephalus rostratus* is expanded when the mouth is opened and contracted when the mouth closes.   A short, strong ligament from the forward portion of the lacrimal (or a pre-lacrimal ossicle, see below) extends anteriorly to an attachment on the top of the maxillary, so that movement of the maxillary must change the position of the lacrimal.   In the preserved specimen at hand, the skin

over the nasal sac is somewhat concave when the mouth is closed, but is drawn taut when the posterior end of the maxillary is moved downward.

Though the method for pumping water over the olfactory rosette is somewhat different from that of most lower teleosts, I think this difference can be sufficiently explained by the exigencies of the relatively long, rather ski-jump shaped snout of *A. rostratus* (Fig. 1).

In contrast with the alepocephalids described above, there appears to be on one side of a relatively undamaged specimen of *Bathylaco nigricans* the usual isospondylous antorbital-supraorbital strut (see Fig. 6c). In view of the shorter snout of *Bathylaco*, as compared with *Alepocephalus*, a more normal olfactory apparatus might be expected.

The lateralis system of the head. The infraorbital canal of *Alepocephalus rostratus* commences at the front of the lacrimal in an upturned tubule. In some specimens this upturned tubule occurs in a separate ossification, but this separate element would seem to be a broken piece of the lacrimal rather than an independent rostral bone. I can find no continuation of this upturned tubule in the skin of the snout or in the dermal portion of the median ethmoid bone. Behind the lacrimal, the infraorbital canal continues around the eye in a series of weak, tubular ossicles, seven on one side and eight on the other. The central ossicles of this series have slight laminar bases but the terminal ones do not. Behind the eye these ossicles are well separated from the orbital border, with cheek musculature extending forward below them. The uppermost (dermosphenotic) is loosely attached to the autosphenotic by membrane. Above the dermosphenotic the infraorbital canal is continued as a membranous tube which barely meets the tip of a forward projection, also in a membranous tube, of the temporal canal. The infraorbital system of *A. rostratus* has been adequately illustrated by Gegenbaur (1878, pl. 2, fig. 8).

The supraorbital canal begins at the front of the very long nasal bones, which are primarily tubular and lie alongside the upper portion of the ethmoid region of the skull. After a hiatus between the nasal and frontal bones, the canals continue to the back of the frontals, where they end.

The mandibular-preopercular canal runs its usual course from the front of the dentary to a tubular extension from the top of the preopercle. From there it proceeds via a membranous extension to a junction with the temporal canal. There is no suprapreopercular ossification.

The temporal canal extends back in the dermopterotic to a point just anterior to the preopercular canal where it drops down to a Y-shaped junction with that canal, thence back up again into a short section of the dermopterotic and out the rear of that bone. From the membranous section of the temporal canal behind the dermopterotic the supratemporal commissure extends at right angles over the skull roof. The supratemporal commissure is mostly contained in two small, tubular ossicles (see Fig. 9,Es) before ending blindly. The lateral of these two ossicles is underlain by a fleshy area, but the medial overlaps the parietal from which it is separated by membrane.

From behind its junction with the supratemporal commissure the temporal canal passes back through a small, straight, tubular ossicle and then through an ossicle

movably attached to the base of the posttemporal (Fig. 9,Ll). In this ossicle the canal forms a downward bend, passing thence along the supracleithrum and out onto the body (Fig. 12,ll). The fact that the lateralis and dermal components are separate in the posttemporal (but not in the supracleithrum) in *A. rostratus* is peculiar, perhaps significant.

The relative expansion of the lateralis system in *Searsia koefoedi* as compared to *Alepocephalus rostratus* has already been noted. In *Searsia koefoedi*, the supra-orbital canal is continuous from the nasals through the frontals to a posterior junction with the canals of the supratemporal commissure. In *S. koefoedi* I can find no ethmoidal or frontal commissure, there is no junction of the infraorbital and supra-orbital canals, and the supratemporal canals of the two sides do not meet on the middorsal line. Nor have I observed any of the features mentioned in the last sentence in other alepocephaloids. So far as the systematic position of the alepo-cephaloids is concerned, the lack of an ethmoid commissure and the failure of the infraorbital and supraorbital canals to meet would seem to be the most significant features of the lateralis system of the head.

The jaws and jaw mechanisms

The lower jaw is long in *Alepocephalus rostratus*. It retains three areas of cartilage on its inner face (Fig. 2). Two of these are associated with the articular (angular of
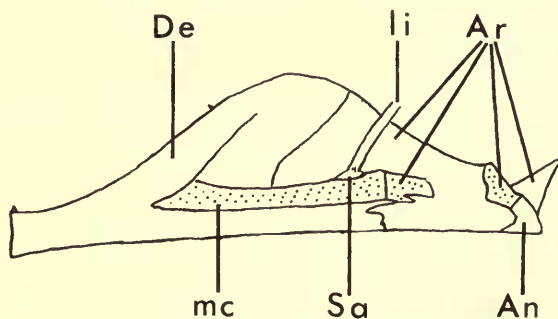
FIG. 2. Right mandible of *Alepocephalus rostratus*, internal view. Only the anteriormost and posteriormost teeth are indicated. Cartilage stippled.

Haines, etc.). One extends upward and forward from a lobe on the angular to the base of the articular-quadrate junction. The other is the endosteal process of Starks (1916, p. 6) which extends forward to Meckel's cartilage. The latter is a strut, somewhat thicker at the two ends, extending between a posterior abutment against the endosteal process of the articular and a forward enclosure by the dentary. The sesamoid articular (Fig. 2,Sa) is a small bone on the upper surface of Meckel's cartilage; it has no other attachment and nowhere meets the articular in the undried fish.

The mouth is closed by means of contraction of the adductor mandibulae. The adductor has its insertion on the inner surface of the articular with a major concen-

tration of musculature attached by ligament (Fig. 2,li) to the sesamoid articular. Posteriorly, the adductor originates on the outer surface of the suspensorium. The surface of attachment extends across the quadrate and the lower portion of the metapterygoid onto the hyomandibular; there is very little attachment surface on the preopercle.

The apparatus for lowering the mandible of *Alepocephalus rostratus* is peculiar. Not one but rather two separate ligaments are attached to the rear of the angular. The upper of these passes directly up and back to an attachment on the outer face of the epihyal. The lower of the two passes back to an attachment near the front of the interopercle, along the upper, inner face of that bone for a short distance, and then leaves it to pass inward and upward to an attachment on the outer surface of the epihyal just below that of the upper angular-epihyal ligament. Posteriorly, the interopercle of *Alepocephalus* has a well-defined membranous attachment to the subopercle which in turn is closely attached by membrane to the under surface of the opercle. The upper surface of the opercle in turn has a well-developed levator operculi muscle which extends anterodorsally to an attachment on the pterotic. It therefore seems that contraction of the levator operculi would serve to lower the mandible as described by van Dobben (1935) by pulling back on the lower of the two ligaments to the angular. It also appears that backward or outward move-ment of the epihyal would accomplish the same thing (Kirkhoff, 1958 : 524) by a backward pull on the upper of the two ligaments to the angular. This double mechanism for opening the mouth seems to be normal in living lower teleosts; at least I have found variants of it in *Elops*, *Albula*, *Chanos*, *Osmerus*, *Salmo*, *Chirocentrus*, and *Clupea*.

In the holostean *Amia* there is a single strong ligament (lmh of Allis, 1897, pl. 19, fig. 2) extending freely between the interopercle (externally) and the outermost branchiostegal ray (internally) to an attachment on the outer face of the epihyal. The forward end of the interopercle is merely attached by loose membrane to the articular area of the mandible above the angular, whereas the outermost branchio-stegal ray is equally firmly attached to the articular area of the mandible below the angular. In *Amia*, then, the interopercle has no special attachment to the mandible and none whatever to the angular; it appears to act merely as the uppermost member of the branchiostegal series (McAllister, 1968 : 4).

It would seem, from the condition described in *Amia*, that (1) retraction or expan-sion of the rear portion of the hyoid arches plays the primary role in lowering the mandible of that fish, (2) that the angular may have arisen as a source of attachment for the epihyal-angular ligament, and (3) that the interopercle can have little to do with the opening of the mouth. From this it appears probable that the incorporation of the interopercle into the mechanism for opening the mouth has arisen in the Teleostei, either by attachment of the interopercle to all or to a portion of the angular-epihyal ligament. *Alepocephalus* differs from other teleosts investigated in having the angular-epihyal ligament divided into two completely separate parts, one attached to the interopercle and one not. In this separation *Alepocephalus* only differs in degree, however, from the condition seen in *Osteoglossum*, and for that matter from other lower teleosts.

Among the various alepocephaloids the ligamentous attachment of the angular and the mechanism for opening the mouth differ among the forms examined. *Bathylaco* shows the typical teleostean condition with a single ligament extending back to the interopercle. *Alepocephalus rostratus* shows the double attachment already noted. *Xenodermichthys socialis* shows a further specialization of the *Alepocephalus* condition in that the subopercle has become reduced to a small strut that does not meet the interopercle at all (Fig. 3A). In this fish, as in *Amia*, the interopercle cannot serve as a mechanism for lowering the mandible. However, the opercular apparatus of *Xenodermichthys* is of a highly specialized construction, presumably arising from an *Alepocephalus*-like opercular type, and is hence most probably a secondary development within the alepocephaloids. A far more normal type of opercular apparatus, differing from that of *Amia* most significantly in the presence of an angular-interopercle ligament, is that found in *Searsia koefoedi* (Fig. 3B).
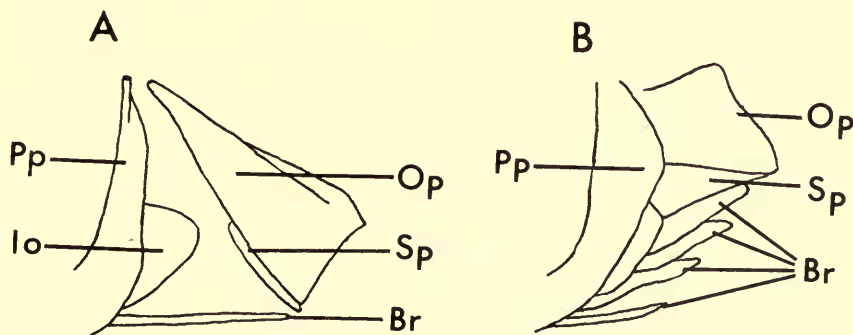
FIG. 3.   Left gill cover, external view, of (A) *Xenodermichthys socialis* and (B) *Searsia koefoedi*.

The upper jaw of *Alepocephalus rostratus* consists, on each side, of a short pre-maxillary, a much longer maxillary, and two supramaxillaries. The premaxillary and maxillary bear short teeth. The maxillary has two articular facets, both on its mesial surface anteriorly. The forward of these props the maxillary against the ethmoid cartilage and the posterior against the cartilaginous tip of the autopalatine (Fig. 4A). Anterior to its front articular facet, the maxillary thins into a vertically flattened wedge extending somewhat between the premaxillary and the ethmoid.

In the alepocephaloids examined, the condition of the premaxillaries varies considerably. Among certain searsids, at the one extreme, the premaxillaries form a sort of a cap over the front of the snout, and have forwardly projecting tusks (see Parr, 1960). At the other, represented by *Bathyprion*, the ethmoid region projects well forward of and between the premaxillaries (Marshall, 1966).

In *Alepocephalus rostratus* the posterior end of the maxillary is membranously connected with the outer surface of the mandible, and when this is lowered the lateral end of the maxillary moves down with it. Stretching of the maxillary-mandibular membrane when the mouth is opened also has the effect of pulling

C

upward the anterior end of the posterior supramaxillary in typically "clupeoid" fashion.

There is also a long ligament (Fig. 4A) extending back from the outer surface of the maxillary anteriorly into the membrane attached to the lower jaw. When the mandible is lowered the shortening of this ligament presumably rolls the lower edge of the maxillary outward (van Dobben, 1935).

Lowering and rolling of the maxillary must transfer some motion of the same sort to the premaxillaries. In addition to the usual (but rather tight) membranous attachment of the premaxillaries to the ethmoid block anteriorly, there are ligaments extending from the fronts of ridges running anterolaterally on each side of the ethmoid to the lateral portions of the premaxillaries (Fig. 4A); these ligaments would prevent lowering of the premaxillaries but would permit an outward rolling of their lower rims.
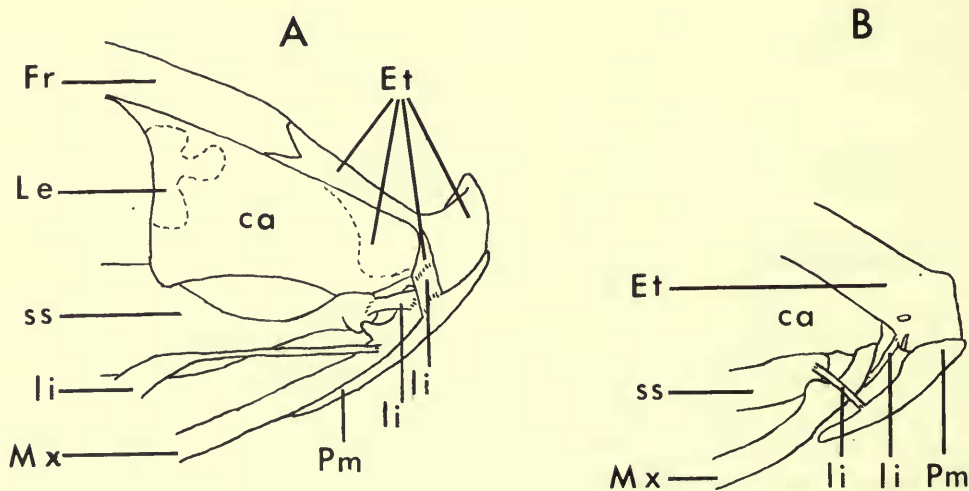
FIG. 4.   Lateral and slightly superior views of the ethmoid region and forward ends of the suspensorium and upper jaw bones of (A) *Alepocephalus rostratus* and (B) *Elops saurus*.

The ligaments that extend from the lateral ridges of the ethmoid out onto the upper surface of the lateral portion of the premaxillaries must also serve the function of holding in place the maxillary heads, for these extend forward to this point between the ethmoid and the premaxillaries. Additionally, there are ligaments from the maxillary heads to the palatines (Fig. 4A). However well this system may serve *Alepocephalus*, it is the reverse of the usual system of ligaments in teleosts, where that from the palatine to the *premaxillary* crosses over another from the ethmoid to the maxillary (see, for example, Gosline, 1961, fig. 8c and p. 32).

The origin of these crossed ligaments can I think be traced back via *Elops* and *Megalops*. In *Alepocephalus* the tough, membranous tissue between the premaxillary and maxillary extends forward to the ethmoid. In this area in *Elops* (Fig. 4B) there is a tendon which, however, extends between the premaxillary and maxillary out

to an eventual attachment on the lower surface of the maxillary. This I think is the ethmoid-maxillary ligament of higher teleosts, the ethmoid-premaxillary ligament of *Alepocephalus* having disappeared. In *Megalops* the ethmoid-maxillary ligament is present, but in addition the premaxillaries have developed dorsal laminae which extend farther up over the rostrum than the premaxillaries of *Elops*. As a result a lateral portion of the premaxillary dorsal lamina is almost in contact with the outer surface of the palatine head, and a strong membrane or ligament is present between them. If this is the correct source for the palatine-premaxillary ligament (Fig. 4B), it has no homologue in *Alepocephalus*. Whether other alepocephaloids have such a ligament I was unable to determine.
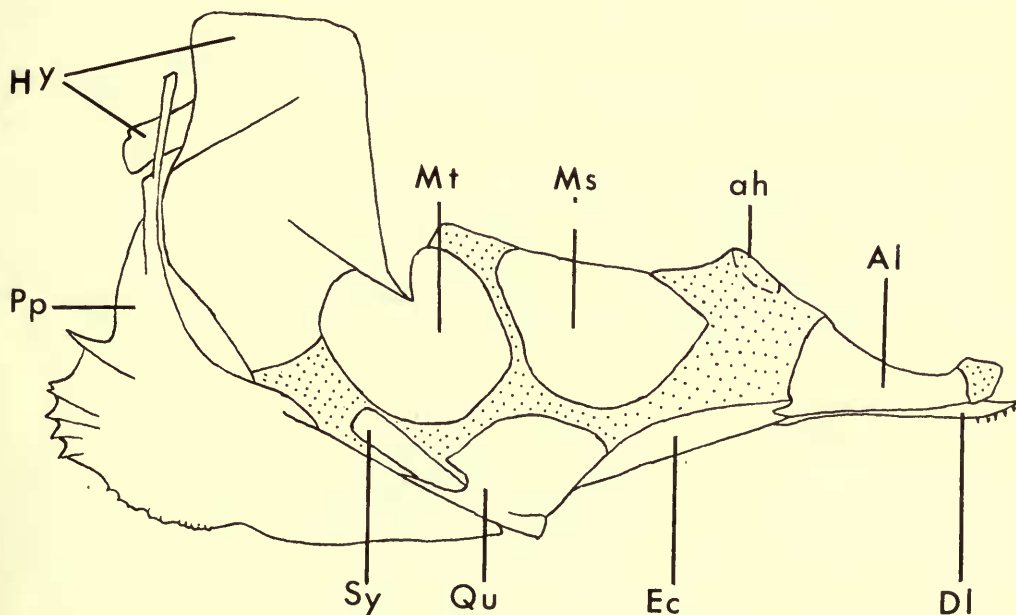
FIG. 5.   External view of right half of suspensorium of *Alepocephalus rostratus*.   Cartilage stippled.

The suspensorium

The autopalatine and (toothed) dermopalatine are represented by separate bones in *Alepocephalus rostratus* (Fig. 5). The dermopalatine is merely a toothed plate which extends inward beyond the autopalatine to nearly meet its fellow on the midline. The autopalatines are continued forward by a nodule of cartilage which extends between the ethmoid block and the articular head of the maxillary (Fig. 4A).

The anterior end of the ectopterygoid wedges slightly between the posterior ends of the dermopalatine and the autopalatine. The large mesopterygoid is toothless and completely surrounded by cartilage. Its upper edge extends inward nearly to the parasphenoid ; this edge is continued posteriorly by a squarish cartilaginous lamina. The metapterygoid is a circular bone with a deep wedge missing. Anterior to this wedge, the metapterygoid forms a continuous, more or less horizontal surface

with the infolded mesopterygoid.   Posterior to the wedge the metapterygoid forms
a continuous vertical surface with the hyomandibular.   The hyomandibular articu-
lates with the cranium by a single, broad head. Posteriorly it gives off a long strut
against which the operculum articulates.

External to its hyomandibular articulation, the operculum has a bony flange
which serves for the attachment of the dilatator operculi muscle.   This muscle
extends forward and upward to an attachment on the pterotic.   The elevator
operculi extends from the upper surface of the operculum upward to an attachment
on the pterotic behind the dilatator operculi.

Perhaps the most notable feature about the suspensorium of *Alepocephalus*
rostratus is the separate autopalatine and dermopalatine.   This occurs elsewhere
among living teleosts only, to my knowledge, in the elopoids (Gosline, 1961).   Pos-
sibly, however, this separation of the two palatine elements in *Alepocephalus* has
developed secondarily in association with the general reduction in ossification in
this fish.

Alepocephalus rostratus has no basipterygoid process, though the block of cartilage
posterior to the mesopterygoid suggests the rudiment of such a process.   In *Searsia*
koefoedi there is a single row of large, well-spaced teeth on the inner border of the
mesopterygoid, and the cartilaginous area behind the mesopterygoid appears to be
propped against (or perhaps between) a pair of knob-like projections from the para-
sphenoid.   In short, *Searsia koefoedi* appears to have a basipterygoid process.

The cranium

Rostral region.   The rostrum of *Alepocephalus* consists primarily of cartilage
(Gegenbaur, 1878, pl. 1, fig. 5).   At its flattened tip the snout forms sort of a sand-
wich of cartilage between two dermal bones—a dermethmoid above and the vomer
below.   The dermethmoid lies entirely superficial to the cartilage.   Possibly the
posterolateral portions of the ethmoid ossification, included in the dashed line in
Fig. 4A, represent an endochondral element, for they contain no superficial irregulari-
ties and stain less deeply than the central portion, but they, too, merely form a thin
cap over the ethmoid cartilage below.   Posterodorsally the dermethmoid inter-
digitates with the anterior end of the frontals.   The front of the median, toothless
vomer extends almost to the snout tip at the midline.   More posteriorly it spreads
out as a thin, flat plate on the lower surface of the ethmoid cartilage, passing back
ventral to the parasphenoid. The anterior ends of the dermopalatines swing medially
below the vomer.   However, the cartilaginous anterior tip of the autopalatine
articulates with the ethmoid cartilage above and lateral to the vomer.

Posteriorly the ethmoid cartilage forms two vertical, lateral struts.   Embedded
in these, and reaching neither the frontals above nor the parasphenoid below, are
the completely endochondral lateral ethmoids (Fig. 4A).   Each lateral ethmoid
above borders the opening through which the olfactory nerve passes.

The lower surface of each lateral strut forms a cartilaginous facet for the articula-
tion of the cartilaginous upper surface of the suspensorium between the autopalatines
and the mesopterygoid (Fig. 5,ah).

The posterior faces of the lateral cartilaginous struts form the anterior borders for the eyeball.   On the midline the cartilaginous ethmoidal block extends somewhat posteriorly to the lateral flanges.   This median area contains two anterior myodomes, one above the other.   Between the two, the cartilage projects posteriorly and forms the surface for attachment of a median, ligament-like membrane that extends up and back to a forward projection of the median orbitosphenoid.

Skull roof.   The skull roof of *Alepocephalus rostratus* has been illustrated by Gegenbaur (1878, pl. 1, fig. 3) and this figure appears redrawn in Gregory (1933, fig. 51).   Unfortunately it is badly in error with regard to the bones on the parietal-epiotic region.
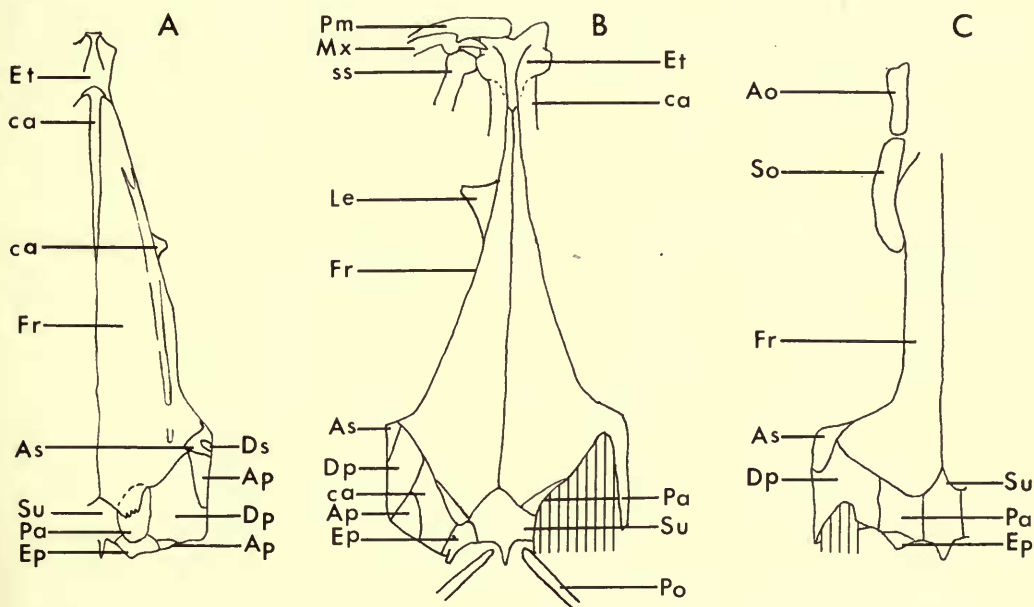
FIG. 6.   Skull roofs, from above, of (A) right half of *Alepocephalus macropterus*, with the course of the lateral line indicated ; (B) *Xenodermichthys socialis*, with the forward ends of the left suspensorium and upper jaw bones and the posttemporals shown ; and (c) the left half of *Bathylaco nigricans* with the approximate position of the presumed antorbital-supraorbital strut indicated.   The forward ends of the epaxial musculature are shown by parallel lines on the right half of (B) and in (C).

The frontals are much the largest bones on the skull roof (Fig. 6).   At the back of the orbital rim they slightly overlap the upper portion of the autosphenotic.   More posterolaterally the frontals form a continuous border with the dermopterotics. Posteriorly the frontals overlap the parietals and supraoccipital.

The dermopterotic of *Alepocephalus* is a thin sheet of bone overlapping, but separate from the autopterotic.   Aside from the frontals the dermopterotics are the largest bones on the skull roof.   Anteriorly, they extend over the autosphenotics. Laterally, they extend to the posterolateral angle of the skull roof, though ahead of that a small part of the autopterotic, above that portion that forms the posterior

half of the hyomandibular facet, is exposed (Fig. 6A,Ap).   (The autopterotic also
extends somewhat behind the level of the dermopterotic on the posterior face of the
skull.)   Medially, the dermopterotics border the frontals and parietals.

The supraoccipital, though quite small, completely separates the parietals.   It
has three short, parallel ridges on its dorsal surface, which presumably represent a
dermal component.   The parietals extend under the frontals anteriorly and over the
epiotics posteriorly.   The epiotics, despite Gegenbaur and Gregory (see above), do
not form part of the skull roof though they protrude somewhat posteriorly on the
posterior face of the cranium.

The floor of the cranium.   The parasphenoid is a long bone, passing between the
vomer and the ethmoid cartilage forward and extending under the basioccipital
posteriorly (Fig. 7).   Under the posteroventral border of the orbits, there are slight
dorsolateral flanges on the parasphenoid that extend out in front of the prootics.
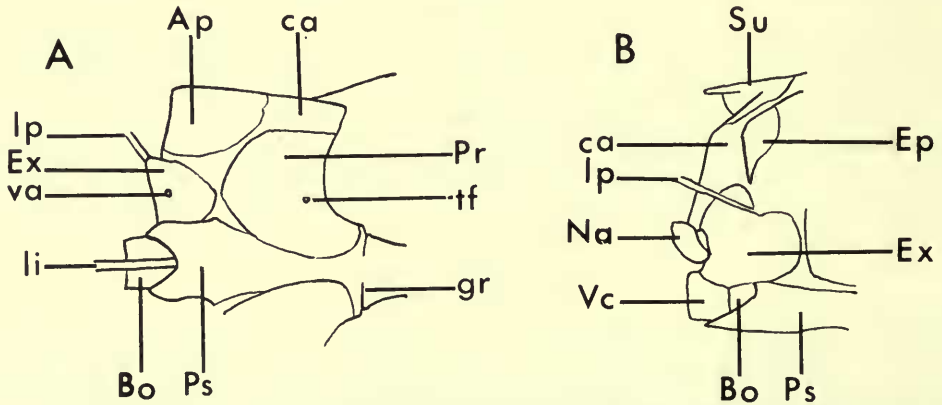
FIG. 7.   Posterior portion of right half of cranium of *Alepocephalus rostratus* from (A) below,
and (B) the side.

On the ventral surface of these flanges there is, on each side, a groove (Fig. 7A,gr)
that extends at right angles to the longitudinal shaft of the parasphenoid. These
grooves serve for the attachment of muscles which, on contracting, pull the suspen-
sorium in toward the parasphenoid.   Posteriorly, a ligament issues from the space
between the parasphenoid and the basioccipital and passes back below the vertebral
column (Fig. 7A).

Sphenoid region.   Posteromedially the orbits are bordered by the median orbito-
sphenoid and the paired pterosphenoids (Gegenbaur, 1878, pl 1, fig. 4).   The olfactory
nerves pass forward from a median hole between the front end of the orbitosphenoid,
which is V-shaped in cross section, and the cartilage above it.   The endochondral
pterosphenoids meet one another below anteriorly but not posteriorly.   Anteriorly
the pterosphenoids meet the orbitosphenoids.   Above they meet lightly ossified
flanges of the frontals which extend down over much of the posterodorsal surface of
the orbit.   Posterodorsally each pterosphenoid is separated from the sphenotic by
cartilage ; posteriorly it nearly meets the prootic ; and posteroventrally it is slightly
separated from the wing of the basisphenoid.   The basisphenoid wings, which meet

one another on the midline, seem to form the principal sources of attachment for two of the eye muscles. The basal median strut of the basisphenoid appears to be variously developed in different specimens of *Alepocephalus rostratus*. Gegenbaur (1878) describes and figures a rather well-developed median strut. A similar strut seems to be represented in the two prepared skeletons available. However, in the wet specimen I can find only an unossified ligament where the strut should be.

Otic region. The autosphenotic is a relatively large bone at the posterodorsal corner of the orbital border. Above and anteriorly it is overlapped by the frontal. Posteriorly it meets the autopterotic. Below, it extends to the upper border of the anterior portion of the socket for the hyomandibular articulation. The socket itself is cartilaginous anteriorly (Fig. 8,hs).

The prootic forms the lower border of the anterior portion of the socket for the hyomandibular. Anteriorly it extends into the orbit, bordering both the pterosphenoids and the basisphenoid. The trigeminal-facialis nerve has a single opening in the orbital face of the prootic, then a branch passes through a hole in the rim to exit on the lateral face of the same bone (Fig. 7A,tf). Ventrally the prootic meets the parasphenoid.

The posterior face of the skull. The supraoccipital does not extend down far on the posterior face of the skull, so that the central section down to the border of the foramen magnum is cartilaginous (Fig. 7B). The rims of the foramen magnum are bordered anterolaterally by the exoccipitals. These have no facets for vertebral articulation. However, they have lower facet-like projections into the upper surface of a part of the posterior portion of the basioccipital (?) that looks very much like an anterior vertebra that has become fused to the skull (Fig. 7B,Vc). Ridewood (1904, p. 64) notes this same inclusion of a half vertebra into the basioccipital of *Amia* and *Megalops*. Posterolaterally the foramen magnum is covered on either side by small, separate plates (Fig. 7B,Na) that doubtless represent the neural arches of the centrum that has become fused to the skull.

There are no fossae of any sort on the posterior or inferior faces of the skull. The inferior face of the exoccipital is, however, evenly concave forming a shallow cavity into which the large mass of hypaxial muscle fits (Fig. 8).

Attachments of body musculature to the skull

Hypaxial musculature in Alepocephalus rostratus. In *Alepocephalus rostratus* a large mass of hypaxial body musculature extends forward underneath the cranium on either side of the parasphenoid (Fig. 8). The attachment surface for this musculature is made up principally by the exoccipitals medial to the exit of the vagus nerve and the whole posterior portion of the prootic. The vagus nerve, after exiting from the exoccipital (Fig. 7A,va), passes laterally over the dorsal surface of this musculature, thence downward over its surface.

I can find no comparable expansion of musculature under the skull of other fishes, though I have not examined other deep water forms where, possibly, it is an adaptive feature. In the holostean *Amia* a similar muscle extends in over the lower surface of the skull. It extends forward slightly over and slightly under the vagus nerve

(Allis, 1897, e.g., pl. 12, fig. 35). Ventrally this muscle in *Amia* extends forward onto the cartilage slightly ahead of the basioccipital, but ends far short of the prootic.

Among the teleosts examined, the elopoid *Albula* and the salmonoids *Argentina* and *Salmo* have this muscle extending forward on the lower surface of the skull about as in *Amia*. In the gonorhynchoid *Chanos* there seem to be several ligaments passing forward onto the under surface of the cranium but no musculature. In the elopoid *Megalops*, the body musculature to the lower face of the skull is restricted anteriorly to the area behind the gas bladder diverticula but expanded laterally as in *Alepocephalus*. In the clupeoid *Clupea* there is a very slight sheath of musculature extending outside of the gas bladder extension to an attachment on the skull anterior to the diverticulum; behind the diverticulum the attachments to the skull are principally ligaments with a slight amount of musculature interspersed.

From a priori considerations it seems that large muscle masses to the under surface of the skull and a connection between the gas bladder and the inner ear could not
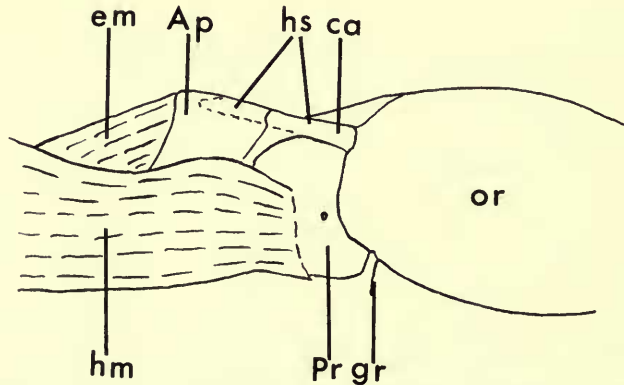
FIG. 8.   Attachment of the body musculature, indicated by dashed lines, to the right half
of the skull of *Alepocephalus rostratus*, from below.

effectively occur in the same fish. Possibly the great expansion of the hypaxial musculature to the skull in *Alepocephalus* is related to its loss of a gas bladder.

Epaxial musculature in Alepocephalus rostratus. The relationship between the body musculature and the top portion of the cranium is more complicated (Fig. 9). Starting on the midline, the supraoccipital furnishes attachment for ligamentous tissue which leads into a band of musculature extending down the midline of the back (Fig. 9,mu). The dorsal wing of the posttemporal extends in over the dorsal surface of the nape almost to the supraoccipital. It has no direct articulation with the cranium ; however, there is a strong ligament passing laterally from its tip to the posterodorsal surface of the epiotic. The attachments to the posterior edge of the posttemporal wing are of two types. Medially a ligament passes back into musculature which joins mostly the middorsal band but partly the epaxial body musculature. More laterally the posttemporal forms a rim for attachment of a thin sheet of epaxial body musculature (Fig. 9,mp).

Extending forward below the sheet of epaxial musculature to the posttemporal is another section of epaxial musculature that attaches to the back of the skull (Fig. 9,me). This portion passes in below the posttemporal-epiotic ligament medially but also around the epiotic end of this ligament to an attachment somewhat farther forward on the skull roof, just about reaching to below the lateral extrascapular (Fig. 9).

The deep fork of the posttemporal, continued as a ligament to the exoccipital (Fig. 7,lp), divides this portion of the epaxial musculature from a still more lateral portion which passes forward external to the deep fork to an attachment on the posterolateral face of the cranium (Fig. 9,ma). (This lateralmost portion also has a strong membranous connection to the inner surface of the posterolateral end of the posttemporal.) Anteriorly this lateral portion extends forward below the level of the main portion of the lateral line to an attachment on the cranium only slightly ahead of the level of the extrascapular ossicles (Fig. 9).
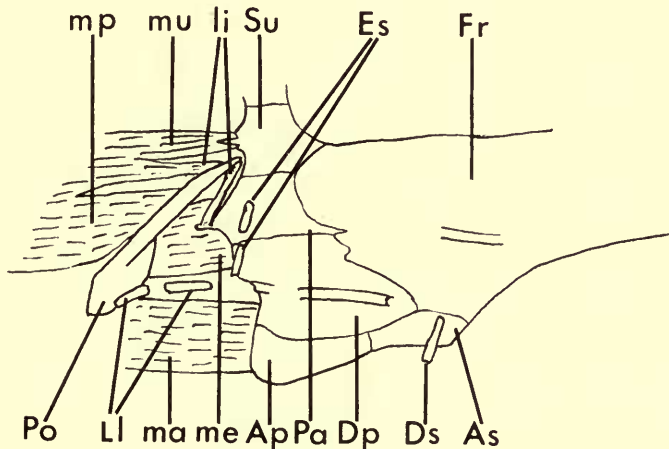
FIG. 9.   Attachment of the body musculature, indicated by dashed lines, to the skull and posttemporal bone of the right side of *Alepocephalus rostratus*, from above.

The forward portion of the epaxial musculature can thus be divided into three parts depending on their relations to the posttemporal : (1) a superficial sheath attached to the upper wing of the posttemporal, (2) a deeper medial portion passing to the skull below the upper wing of the posttemporal and internal to its deep strut, and (3) a lateral portion passing forward to the skull external to the deep wing of the posttemporal. All three of these portions merge posteriorly into the epaxial body musculature.

The relationship between body muscle attachments and skull bones in actinopterygian fishes.   In *Alepocephalus rostratus*, as already noted, there is no posttemporal fossa and very little epaxial musculature passing forward over the skull roof ; on the other hand this fish has a great mass of hypaxial musculature extending far in under the floor of the skull. This is a most unusual, perhaps unique, arrangement. However, the nature of the skull bones to which the body muscles are attached varies considerably among alepocephaloids. Before dealing with these it seems well to review

the history of body muscle attachments to the skull in actinopterygian fishes.

In actinopterygians there has been a progressive specialization in the attachment of the body musculature to the cranium. For one thing, the cranium of higher forms provides greater and firmer sources of muscle attachment than in lower forms. For another, a specialization among the muscles attached to the skull seems to have developed.

In the higher actinopterygians, at least, there seems to be a relationship between concentrations of muscular stress and bone formation, as Gegenbaur (1878) pointed out long ago. Thus in *Amia* the main stress of muscular pull on the head appears to be concentrated into ligaments attached to the epiotics. This is not to say that all muscles attach to bone. Indeed, in *Amia* there are well-developed posttemporal fossae enclosed primarily by cartilage, and muscle attachment is distributed evenly over its surfaces. It is perhaps significant in this regard that the muscle attachments to the walls of the posttemporal fossae of *Chanos* are similar to those of *Amia* but that in *Chanos* an ossified ligament develops in the shaft of the musculature entering the fossa.

An increase in the surface for muscle attachment on the back of the skull in actinopterygians may take place in two ways : (1) by the extension of musculature into fossae in the skull or extension of the body muscles onto the horizontal surfaces of the skull or (2) by backward projections from the skull. The second method of increasing the surface of musculature attachment is well exemplified by the long terminally-frayed projections of the epiotics extending back into the body in *Sphyraena* (Starks, 1899), but occurring in numerous other fishes (see, for example, Ridewood, 1904, pp. 65–66). The functional difference between such osseous brushes projecting back from the skull and an unossified ligament attaching to the rear of the skull would seem to be slight. With regard to extensions of musculature into or over the skull, it may be that extension of musculature under the lower surface of the cranium appeared earliest. At least, it occurs to a moderate degree in *Amia* and many lower teleosts, apparently reaching the epitome of its development in *Alepocephalus*. However, the extent to which this development can occur is limited amongst other things by the gill arch system ; where, as in *Alepocephalus*, there is a large mass of musculature extending in under the skull, the gill arches are necessarily displaced downward and/or laterally, affecting inter alia the gill cover and opercular structure (see Figs. 1, 3A). Muscle encroachment into and over the skull has a longer history which is linked with that of the actinopterygian dermal roof.

In the chondrosteans and holosteans a series of paired dermal bones formed an almost continuous, presumably protective, roof over the head and nape. The bones forming this roof were the nasals, frontals, parietals, extrascapulars, and posttemporals and laterally the dermopterotics (see, e.g., the pholidophoroid *Ichthyokentema*, Griffith and Patterson, 1963, fig. 1). All of these bones were, in addition, canal-bearing ossifications. In the subsequent evolution of fishes the nasals and extrascapulars retained their canal-bearing properties but usually lost their attributes as portions of a continuous, rigid skull roof. The posttemporals have had a more complicated history. They have gradually exchanged their roofing function for that of a movable strut linking and attaching the pectoral girdle to the back of the skull.

An initial step in this direction is seen in *Amia*, where the medial portion of the post-temporal slides in under the extrascapular to form an attachment to the cranium.

Though the medial end of the posttemporal extends nearly to the middorsal line in *Amia* and the lower teleosts, as it did in the lower actinopterygians, it does not form a direct ligamentous attachment between its medial end and the portion of the cranium immediately in front of it.   I believe there is a good functional explanation for this. If such an attachment occurred, any backward pull on the pectoral girdle would cause the lateral end of the posttemporal to swing backward around the medial end as a hinge.   However, in passing from the head onto the body, the main lateral line canal passes across the lateral portion of the posttemporal bone (Fig. 9,Ll), and any extensive backward swinging of the lateral end of the posttemporal would rip apart the main lateralis system.   What occurs even in *Amia* is that the posttemporal develops an axis of rotation nearer to its outer than to its medial end, which results in far less displacement of its lateral portion.   This more lateral axis is brought about by the development of a deep fork of the posttemporal which extends down and in from near the lateral border of the posttemporal to an attachment on the intercalar (or exoccipital in *Alepocephalus*) more or less directly below.   The upper fork of the posttemporal develops a ligamentous attachment not to that portion of the cranium ahead of it but to the epiotic lateral to it (Fig. 9).   These posttemporal attachments continue throughout the main stem of the Teleostei.

The way that the muscular encroachments on the skull of the holosteans and teleosteans have developed on the back and roof of the skull seems to be related to fixed points provided by the posttemporal attachment—the epiotic above and the intercalar below.   Perhaps the earliest encroachment to develop is the roofed post-temporal fossae of *Amia*, *Ichthyokentema*, and many lower teleosts.   These fossae appear to be merely excavations in the back of the skull to increase the surface for muscular attachment.   They lie lateral to the epiotic-intercalar area and seem origin-ally to have been roofed primarily by the dermopterotics.   (In my opinion it is best to restrict the term posttemporal fossae to the *roofed*, lateral excavations found in such fishes as *Amia*, *Elops*, etc.)

A second pair of excavations is found medial to the posttemporal fossae in the back of the skull of such a fish as *Albula*.   These are separated from the posttemporal fossae by a vertical ridge of bone made up of the epiotics above and the intercalars below.   They are divided from one another by a median vertical projection com-prised primarily by the supraoccipital.

The supraoccipital is a median bone that does not occur in *Amia* or lower actino-pterygians.   Nevertheless, the median vertical septum must always have been attached to the skull along the midline.   In the telosts, but not, so far as I can determine, in *Amia*, there is a well-developed middorsal band of muscle more or less separate from the epaxial musculature on either side of it.   This median muscle is attached forward to the supraoccipital, which, in lower teleosts, extends back into it as a vertical crest.   Indeed, in *Chanos* the posterior end of the supraoccipital is splayed out into a vertically aligned brush, presumably to provide a greater surface of attachment for this muscle.   It is this vertical supraoccipital crest which divides the two medial fossae on the back of the skull roof of *Albula*.

The subsequent history of the encroachments of musculature on the skull roofs of teleosts can, I think, be understood in terms of the four excavations in the posterior face of such a fish as *Albula*. The musculature of higher telosts has, as it were, pushed through the roofs of these four fossae and extended forward over the skull. The diminution in area of surface attachment caused by the loss of the roofs of the four fossae has, in the long run, been more than made up in at least many percoids by the development of vertical ridges rising from the skull roof with their lateral attachment surfaces—the supraoccipital crest medially and frontal-parietal crests more laterally. The frontal-parietal crests extend back to over the epiotics, dividing the musculature that extends in over the skull medial to the epiotics from that external to the epiotics.

Even in such a primitive teleost as *Salmo* the roof of the posttemporal fossae is gone and the body musculature extending over the cranium lateral to the epiotics is exposed above. *Salmo* shows, however, no great encroachment by body musculature onto the skull roof medial to the epiotics, though the " shoulders " of the cranium on either side of the cranium are somewhat rounded. Where these medial portions of the body musculature do extend forward onto the cranium there is usually, though not in eels, a concomitant development of a supraoccipital crest extending forward on the cranial roof. When this occurs, the part of the supraoccipital rising above the skull roof serves for the attachment of paired epaxial muscles, not of the median longitudinal muscle.

In light of the above discussion the variations in body musculature attachments and cranial bones in alepocephaloids will be dealt with. The large masses of hypaxial muscle attaching to the floor of the skull in *Alepocephalus rostratus* would seem to reach their extreme development in that fish.

Alepocephaloids show considerable variation in the amount of epaxial musculature extending into or over the upper portion of the skull. In *Alepocephalus rostratus* there are no posttemporal fossae and very little musculature extending over the skull roof. The same is true of *Bathyprion danae*. Both of these forms have, incidentally, very large dermopterotics. In *Bathylaco* (Fig. 6c), the epaxial musculature extends over the skull roof laterally and forward below the dermopterotics, which thus form the roofs of posttemporal fossae. In *Xenodermichthys* (Fig. 6b), this roof is gone, and the dermopterotic is reduced to a relatively small, anterolateral bone.

Certain points about body muscle—cranial bone relationships are brought out by these variations in alepocephaloids. It would seem that when the epaxial musculature extends forwards on the upper portion of the skull, its first extension is into an attachment *below* the dermal covering bones, e.g., to the walls of posttemporal fossae. The attachments of such musculature may be to cartilage or endochondral bone. When the roofs of these fossae are reduced or disappear, the primary effect is a reduction in the extent of dermal roofing elements, e.g., the dermopterotics and parietals in *Xenodermichthys* (Fig. 6b). But even in *Xenodermichthys* the musculature has come to extend to some extent *over* the surface of the dermopterotic. And, of course, in higher teleosts the musculature often extends *over* the parietals and frontals as well.

The gill arches

The gill arch system of *Alepocephalus rostratus* was described in a general way by Gegenbaur (1878). The posterior portion of this system has been discussed by Nelson (1967, pp. 75, 76 and fig. 1b) and the hyoid arch and branchiostegal rays by McAllister (1968, pp. 37, 38).

The hyoid apparatus. In *Alepocephalus rostratus* there are two superficial hypohyal ossifications well separated by cartilage. The upper provides a source of attachment for the ligamentous tissue connecting the hyoid apparatus to the glossohyal and basibranchials, and the lower provides attachment for the ligament to the urohyal. The ceratohyal is considerably narrower in the middle than at either end; it has no foramen and is separated by cartilage from the hypohyals anteriorly and the epihyal posteriorly. The cartilaginous area separating the epi- and ceratohyal is expanded below both bones. The epihyal tapers rather abruptly posteriorly, ending in a cartilaginous nodule which provides a surface for articulation of the interhyal. The interhyal is cartilaginous except for an anterolateral surface ossification to which ligamentous tissue is attached.

There are six, widely spaced branchiostegal rays in *Alepocephalus rostratus*. The anteriormost branchiostegal inserts behind the middle of the ceratohyal. The first two are attached to the base of the ceratohyal medial to the protractor hyoidei muscles (Kirkhoff, 1958) which extend from the symphysis of the mandible back to an insertion on the outside of the ceratohyal slightly behind its middle. The four branchiostegals behind this point are attached to the outer surface of the hyoid arch. The anteriormost of these articulates with the cartilage just below and behind the posteroventral end of the ceratohyal; the posterior three insert on the epihyal. The posterior four branchiostegals are very long and nearly straight, extending back below the subopercle; they are slightly laminar near the base but extend beyond the laminae as long, roundish, flexible struts.

The nature of the branchiostegal rays differs considerably among alepocephaloid fishes. Both the number (4–13) (Marshall, 1966; McAllister, 1968) and the form vary. In alepocephalids the uppermost ray is a long, thin strut which, at least in *Xenodermichthys* (Fig. 3A), seems to form a prop for the lower corner of the opercle. Conversely, in such fishes as *Searsia* (Fig. 3B), the upper branchiostegals are short and lath-like.

The functional gill arches. There are four gill slits. The first three are wide. However the fourth extends up only to about the level of the corner of the arch. From there it extends backward, curving upward, as a closed pocket. This pocket is continuous with the pharynx medially and forms a lateral diverticulum from it on either side. From the front and rear each diverticulum is invaded by large gill rakers that face inward on the front and rear of the diverticulum. The anterior edges of the gill rakers of the back wall intermesh between the posterior edges of the gill rakers of the front wall to more or less completely obliterate the central cavity of each diverticulum. The musculature suggests that the posterior series of gill rakers can be moved in and out of the cavity to form a triturating mechanism.

The internal surface of the mouth in the branchial arch region and elsewhere has

occasional small villi protruding from the surface.   There are also well-developed gill
rakers on the arches, which seem normal and lath-like, not spiniferous.   The only
teeth on the gill arch system are the series of small teeth on the pharyngeal bones,
all of which have backwardly curved, pointed tips.   The teeth on the lower pharyn-
geals and on the first two upper pharyngeal plates are in single rows; those on the
third upper pharyngeal plate are in two or three rows.   Of the plates bearing the
pharyngeal teeth the lower seem to be completely fused to the underlying endo-
chondral bone, the anterior upper plate is closely united to the bone below, and the
posterior two are completely separate.   The relationship between the toothless
dermal plates and the underlying bone is complex.   In the tongue, the dermal
component is separate, forming a V-shaped element with the angle of the V
posterior.   There also appears to be a thin median strut extending forward over the
cartilage from the second basibranchial and another extending between basibran-
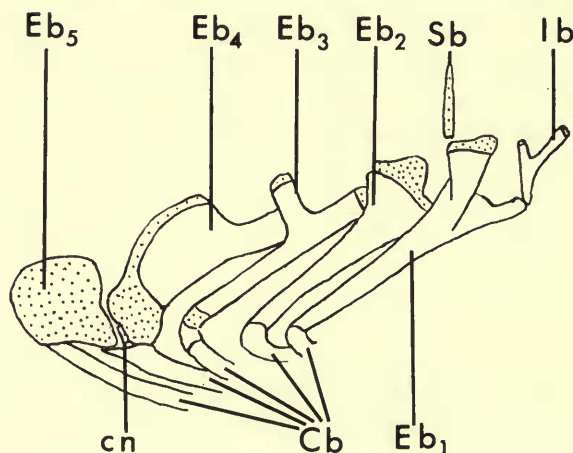

FIG. 10.   Upper portion of the gill arches of right side of *Alepocephalus rostratus*, lateral
view.   Cartilage stippled.

chials two and three, but these seem to be fused to the basibranchials underlying
them.

Endochondral ossifications comprise basibranchials 1 through 4, hypobranchials 1
through 3, ceratobranchials 1 through 5, epibranchials 1 through 4, and infrapharyn-
gobranchials 1 through 3.   Elements that remain entirely cartilaginous are the
suprapharyngobranchial, the large cartilage bordering the epibranchial organ
laterally (Fig. 10, Eb_5), and basibranchial 5.   This last is a very large element,
extending as a long strut posteriorly; basibranchial 5 is, indeed, somewhat longer
than basibranchials 2, 3, and 4 combined.

What is here considered to be epibranchial 5 (see Fig. 10) is a large squarish plate
forming a cap over the lateral end of each pharyngeal diverticulum.   A band of
musculature (not shown in Fig. 10) extends from its posterior surface to the postero-
lateral face of ceratobranchial 5.   There is also a small, free cartilaginous nodule on
the posteroventral surface of each epibranchial 4.   It is possible that these nodules
and not the plates capping the diverticula represent epibranchial 5.

The upper pharyngeal series of the two sides are widely separated from one another on the midline.   The basibranchials form a raised longitudinal ridge.

The same sort of lateral pharyngeal diverticula as those found in *Alepocephalus rostratus* also occur in the alepocephalid *Xenodermichthys socialis*.   However, I did not find them in *Searsia koefoedi*.

The axial skeleton

Anterior vertebrae and associated structures.   Above the front of the anteriormost vertebra is a separate plate-like bone on either side of the nerve cord which bears a slight, posterodorsally projecting spine (Fig. 11, not shown in Fig. 7B).   This is
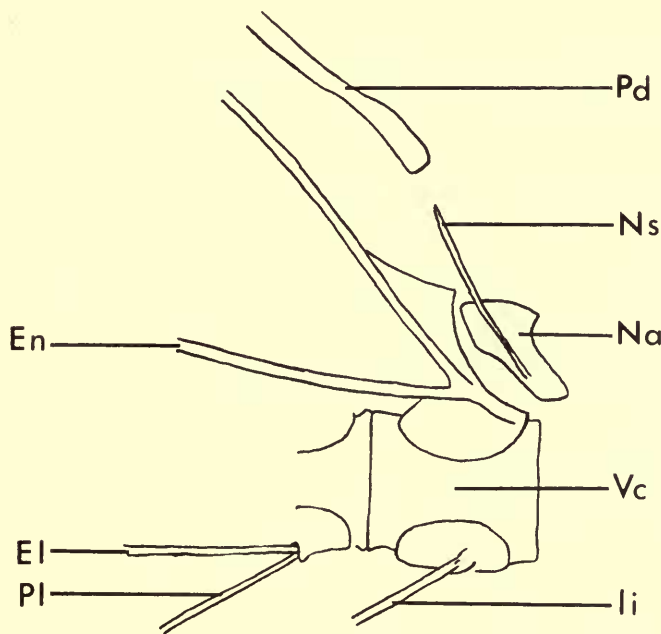

FIG. 11.   Anterior vertebrae and associated structures of *Alepocephalus rostratus*, from the right side.

presumably the neural arch and spine of the centrum that has become fused to the skull (see above).

The anteriormost vertebra is not reduced in size.   Its centrum appears to be mainly or wholly unossified.   Inserted in the centrum are four ossifications, two on either side.   A small knob projects from the ventral one.   To the posterior surface of this knob is attached a ligament that extends back parallel to the pleural rib of the second vertebra (Fig. 11,li).   The dorsal ossification serves as a base for two very long bony but fine projections as well as for a flange that borders the nerve cord. The upper of these projections doubtless represents the neural spine and the lower the epineural intermuscular bone of higher teleosts.

The second vertebra differs from the first in that the ventral projection serves as a

basis for the insertion of two autogenous, backwardly projecting ossifications. Presumably the lower of this pair represents the pleural rib and the upper the epi-pleural. Above, the same two bony projections occur as on the first vertebra, neither of which is autogenous.

Aside from the centrum, the vertebral structures mentioned up to this point are all paired. However, there is also a long median strut extending up and back from above the first neural spine (Fig. 11,Pd). This strut is very long and somewhat anteroposteriorly expanded. At its dorsal end it forms a roundish flat plate on the surface of the flesh just below the skin. Another difference between this median strut and the projections hitherto mentioned is that it is at least partly cartilaginous; in any event the portion just below the superficial plate shatters easily (as cartilage does).

Posterior abdominal vertebrae. At the level of the last two abdominal vertebrae the following changes have taken place as compared with the anterior vertebrae described above. The pleural rib seems to have become fused to its socket and the epipleural rib articulates with the outside surface of the base of the pleural rib. Above, all trace of a plate-like neural arch element seems to have disappeared, leaving only the neural spine and epineural rib united basally with their presumably osseous nodule.

Caudal vertebrae. In the region below the front of the dorsal fin of *Alepocephalus rostratus* the neural and hemal arches pass directly into median spines. The bases of these elements seem to be fused into the centrum. There are no epipleural or epineural elements with bases on the vertebrae in this area.

Farther back, the hemal arches on pre-ural vertebrae 1 and 2 are autogenous, but those farther forward are not. None of the neural arches ahead of the caudal skeleton is autogenous.

Caudal skeleton and caudal fin. The caudal skeleton of *Alepocephalus rostratus* has been illustrated on two occasions (Gosline, 1960; and Patterson, 1968, also in Nielsen and Larsen, 1968, fig. 10) based on a dried preparation in the British Museum. Though this dried skeleton has been well prepared, certain features can be added from the undried dissection.

There are six hypurals, two below and four above. Hypurals three and four have become completely or almost completely united as Patterson's (1968) figure indicates. The last hemal element and the lower three hypurals have cartilaginous caps by means of which they articulate with the centra. The last hemal element articulates with pre-ural centrum 1 and the second hypural with with first ural centrum. The first hypural, which has a well-developed articular head, straddles the area in between. This is not indicated in the dried skeleton, where hypural 1 has a well-developed association with ural 1—see Gosline's or Patteron's illustration. It may be that the two specimens represent individual variations. Or it may be that in drying the base of hypural 1 has shifted backward.

Above the hypurals and below the uroneurals, what is either a sheathed noto-chord or a cartilaginous replacement of it becomes exposed somewhat ahead of the level of the base of the uppermost hypural. From here it extends back free of the uroneurals into the caudal fin. It terminates at a somewhat weakly developed socket

under the base of the lowermost of the upper unbranched rays at about the level at which the ray becomes segmented, i.e., it underlies the unsegmented basal portion. On the surface of the " notochord " behind the second uroneural there are two small, somewhat nodular concretions, possibly UN3 of Gosline and UN3 and 4 of Patterson. However, these concretions differ from the overlapping uroneurals and ray base in being formed in, not outside and separate from, the " notochordal " sheath. (Norden, 1961, p. 709 has described similar nodular formations in the cartilaginous " urostyle " of *Thymallus*.)

There are two pairs of well-developed uroneurals and three epurals. The posterior two epurals are equally long and very roughly parallel. The posterior runs for much of its length between the uroneurals and its anterior portion is not shown by Gosline or Patterson. The anterior epural is small and quite separate. It roughly parallels the posterior neural spine and extends down to just in front of the small neural flange from the first ural vertebra. This flange, which extends between the uroneurals, is median distally but divided proximally, arching over the nerve cord.

I cannot find that the last neural spine or the one previous to it are cartilage-based or autogenous.

In the caudal fin there are 17 branched rays, 9 above and 8 below. The outer principal rays of the caudal fin have ligaments attached to their surfaces part way out along the ray and tapering, more or less pointed bases. The central four rays have expanded, disk-like bases.

On the midline of the caudal peduncle behind the dorsal and anal fin there is a series of flap-like backward extensions that doubtless represent the scale pockets. Sequentially following these is a series of progressively larger accessory rays, 13 above and 15 below. Unlike the dorsal, anal, and principal caudal rays, the anterior accessory rays have no muscle or ligament attachments and no endoskeletal supports. The anterior accessory rays are paired, somewhat tapering, unsegmented, hair-like structures, with the two halves of each element only loosely bound together; only the much heavier, posteriormost accessory rays are segmented.

The pectoral girdle and pectoral fins

The deep arm of the posttemporal very shortly becomes a ligament which passes into what appears to be the posterior rim of the exoccipital. (If there is a separate intercalar I cannot make it out.)

The postcleithrum extends down over, and nearly parallel with the upper portion of the cleithrum (Fig. 12). I can find no indication whatsoever of any postcleithrum. At the upper end of the cleithrum there is a deep notch through which Baudelot's ligament passes from the inside (Fig. 12,bl). From this point Baudelot's ligament passes inward through the hypaxial musculature in close association with one of the intersegmental septa (that between hypaxial myotomes four and five) to an attachment on the side of the first fully developed vertebra.

The uppermost pectoral ray articulates directly with the scapula, or rather with a cartilaginous cap covering the scapular condyle. This condyle is continuous with the rest of the bone and I can see no evidence in the large *Alepocephalus rostratus* of a

separate origin for the scapular condyle. Below the scapular condyle are four actinosts of increasing length. Each of these actinosts consists of bone tipped at either end by cartilage. They do not lie in a single vertical plane basally, though they do distally; rather, the base of the lowermost actinosts extends in to an articulaton somewhat medial to that of the one above it.

Except for the two upper and two lower pectoral rays, the inner (but not the outer) halves of the ray bases insert on cartilaginous nodules (which recall the cartilaginous nodules at the base of the rays of the vertical fins, Fig. 14). There are five of these nodules, and the inner halves of the ray bases ride between them so that there is essentially one per ray. However, the uppermost nodule is somewhat larger than the others and extends under two rays. Under the lowermost ray base there is a heavy bed of membranous tissue, but it seems to contain no cartilaginous nodule.
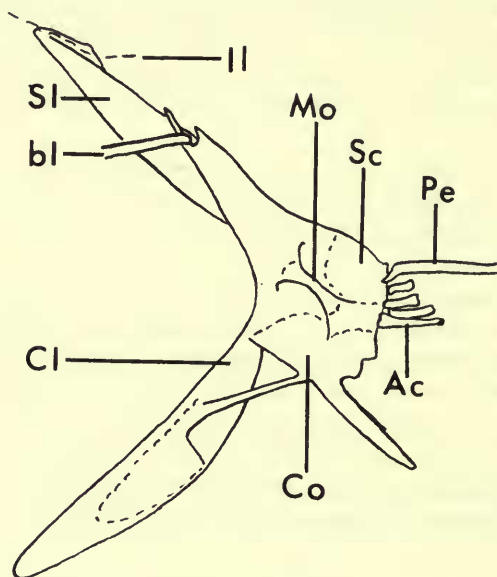

FIG. 12.   Internal view of right side of pectoral girdle of
Alepocephalus rostratus.

There are nine pectoral rays in *A. rostratus*, all segmented and all, except apparently the upper (which is broken), branched. There is no separate splint above the uppermost pectoral ray. However, the base of the uppermost ray is complex and I think it probable that a splint has become fused with its inner " half ". Of the two " halves " that make up the uppermost pectoral ray, the outer is similar to the bases of the outer halves of the rays below and takes no part in the articulation with the scapula. The inner half is broadly tipped with cartilage, which forms the articulating surface of the ray.

The pelvic girdle and associated structures

The pelvic girdle consists of a plate of bone with a long forward strut set in cartilage.

There is also a separate cartilaginous nodule underlying the inner fin rays (Fig. 13). Outside of the outermost fin rays, there is the separate, unarticulated bony strut found in so many lower teleosts (Gosline, 1961). There are seven pelvic rays, all but

Fig. 13.   Right half of pelvic girdle of *Alepocephalus rostratus*, from below.

apparently the outermost branched and all segmented. The innermost articulates basally with the pelvic nodule just lateral to its tip, the next two progressively lower down on the lateral rim of the nodule.

The dorsal and anal fins

The anterior two dorsal rays articulate directly with the first pterygiophore (Fig. 14); they have no lateral flanges. The third and fourth (and presumably succeeding)
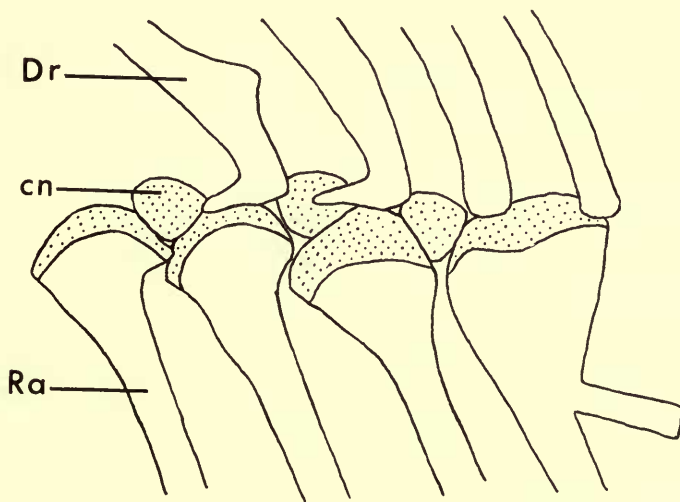

Fig. 14.   Anterior dorsal rays and their endoskeletal supports in *Alepocephalus rostratus*, from right side.   Cartilage stippled.

rays are each inserted between and articulate primarily with nodules of cartilage which in turn interdigitate between the distal heads of the main pterygiophore. The

resemblance between the dorsal and pectoral ray articulations in *Alepocephalus rostratus* has already been noted.

The last two dorsal rays are split to the base.   The last two rays articulate directly with a single expanded pterygiophore.   The ray before the last two articulates with a cartilaginous nodule.

The dorsal pterygiophores are mostly enclosed in the fleshy lobe and do not extend much deeper into the body than the base of this lobe.   The well-developed fleshy lobes at the base of the dorsal and anal fins (Fig. 1) are made up entirely of the musculature to the individual fin rays.   The fin rays themselves are all directed backward, the longer posterior rays more so than the anterior.   The structure of the dorsal and anal fins suggests to me that *Alepocephalus* may use these fins as a major source of normal forward locomotion.

VISCERAL ORGANS

The peritoneum of *Alepocephalus rostratus* is black.   The liver has a single large lobe on the left side with a knob projecting to the right which may represent the right lobe.   The large, heavy-walled oesophagus leads into a U-shaped stomach.   At the pyloric end of the stomach are 18 finger-like caeca.

The bulbus arteriosus of the heart is rather expanded and thin-walled.   I can find find no valves within it.

I did not find the gonads in the specimen of *Alepocephalus rostratus*, but Marshall (1966) has described and figured an ovary and oviduct in *Bathyprion danae*.

LIFE HISTORY

Beebe (1933, pp. 21–56, figs. 2–15) gives an extensive account of the juvenile stages of the searsid genus *Bathytroctes* based on 89 specimens 9·5 to 56 mm. long. These small individuals were essentially like the adults; i.e., development is direct and there is no specialized larval form.   Beebe's specimens were taken in the depth range at which adults occur (500 to 1000 fathoms) suggesting no vertical migration during ontogeny.   His figure of a 9·5 mm. individual (Beebe, 1933, fig. 8A) shows a yolk sac extending for a third of the length of the fish, indicating a very large egg.   In this regard, Nielsen and Larsen (1968, pp. 228–229) report eggs in the female of *Bathylaco nigricans* up to 2·7 mm. in length.   They suggest that *B. nigricans* is an oviparous, non-hermaphroditic species.

SUMMARY OF SALIENT CHARACTERS OF ALEPOCEPHALOID FISHES

Before attempting to assess the systematic position of the alepocephaloid fishes it may be well to summarize what would seem to be the salient characters of the group so far as known.

1. No ethmoidal commissure.

2. Supraorbital canal not joining the infraorbital canal.

3. Two free extrascapulars on each side, the supratemporal commissure incomplete.

4. Lateral line in the posttemporal region borne by a separate ossicle, not by the posttemporal itself.

5. Maxillary included in the gape.

6. Two supramaxillaries.

7. Dermopalatine and autopalatine separate.

8. A basipterygoid process may be present.

9. A single large, apparently dermal ethmoid ossification.

10. Supraoccipital separating the parietals.

11. Musculature for adducting the suspensorium inserting well forward, on the parasphenoid.

12. No subtemporal fossae.

13. A large block of hypaxial musculature attached to the floor of the skull on either side posteriorly.

14. A vertebral centrum fused into the base of the skull posteriorly.

15. A well-developed, cartilaginous suprapharyngobranchial on the first gill arch.

16. Triturating organs formed by the last two gill arches in lateral diverticula of the pharynx in some.

17. Neural spine and epineural elements arising from a common osseous base.

18. Pleural and epipleural ribs from the second complete vertebra.

19. Caudal skeleton with the anterior uroneural extending forward onto the second preural centrum.

20. Pectoral actinosts bordered externally by five cartilaginous nodules which are essentially interradial.

21. Mesocoracoid present.

22. Pelvic girdle with a single cartilaginous nodule, with which the three innermost pelvic rays articulate.

23. Dorsal fin inserted well back on the body.

24. No adipose fin.

25. No swim bladder.

26. A relatively large egg; no specialized larval form.

27. No vertical migration during ontogeny.

THE RELATIONSHIPS AND A PROVISIONAL DEFINITION OF THE ALEPOCEPHALOID FISHES

Characters that would seem to represent portions of a common teleostean heritage are retained here and there among various living groups. A relatively high number of such characters occurs among alepocephaloids, e.g., the absence of a junction between supraorbital and infraorbital lateralis canals, the maxillary included in the gape and with two supramaxillaries, the separation between autopalatine and dermopalatine and between autopterotic and dermopterotic, the basipterygoid process, the suprapharyngobranchial element, the epibranchial organ, the neural spine and epineural bone arising from the same basal plate, the anterior uroneural of the caudal skeleton extending forward on to the second pre-ural centrum, the meso-coracoid arch, and the cartilaginous nodule at the base of the inner pelvic rays.

These characters show clearly that the alepocephaloids belong among the basal groups of living teleosts. However, they do not indicate which of the other basal

groups the alepocephaloids are most closely related to. In the first place, these presumably ancestral alepocephaloid traits are distributed among other lower teleosts in a rather haphazard manner. The basipterygoid process is found elsewhere today only among the osteoglossoid fishes; other such features occur elsewhere among elopoids, clupeoids, gonorhynchoids, or/and salmonoids, etc. In any event Ridewood (1904), Hennig (1966), and a host of others have pointed out that relationships cannot satisfactorily be determined on the basis of ancestral characters. Such features, which two or more groups happen to have retained, can at best suggest ways in which these forms have not evolved.

As to ways in which the alepocephaloids have evolved, these seem to be few. The alepocephaloids appear to represent an old, generalized teleostean stock that has taken up an oceanic, midwater existence, and such specializations as they do have appear to be adaptations for that existence.

Thus the alepocephaloids may possess bioluminescent organs of various types, the most notable of which is the shoulder organ of the Searsidae (Parr, 1951, 1960). Neither this, which appears to be unique among fishes, nor the various other light organs more rarely represented among alepocephaloids (Parr, 1960), seems to provide clues concerning relationships.

Alepocephaloids have no swimbladder. However, this structure has been repeatedly lost in midwater fishes (Denton & Marshall, 1958). Again, little indication of relationship is provided. Probably the most that can be said is that groups without swimbladders are not usually closely related to forms that have gone to the trouble of developing these structures into specialized sound amplifiers.

Denton & Marshall (1958) have concluded that alepocephaloid structure is such as to preclude strong, continuous swimming, but that those fishes may effectively dart short distances. For a mode of life of this sort abrupt acceleration from a standing start is advantageous. This would seem to be facilitated by a concentration of vertical fins at the rear of the body. Such a fin configuration and, presumably, mode of life have been adopted by fishes in various environments, e.g., *Esox*, *Sphyraena*, but seem to be particularly common among bathypelagic forms, where, as in alepocephaloids, the dorsal fin is often far back on the body. Thus, the posteriorly placed dorsal fin of alepocephaloids is not unique or diagnostic. However, it seems to provide as good a starting point as any for a discussion of alepocephaloid relationships.

Aleev (1963) has pointed out that the dorsal fin may play one or more of four possible roles: (1) it may provide a keel to prevent sideslipping when a fish is making a turn; (2) it may serve to stabilize forward trajectory (as the feathers on an arrow do); (3) it may act as a rudder to aid in steering; and/or (4) it may aid in forward propulsion. The keel function seems to differ from the other three in several respects. In the first place, the tendency to overshoot a turn depends on forward momentum, which increases with size and forward speed of the fish. Small or slowly moving fishes would seem to have little need for keels. But if a keel is needed, the most effective place for it is over (or under) the centre of gravity. On the other hand, with certain exceptions rudders become more effective with increasing distance from the centre of gravity, and stabilizers and locomotor organs if placed posteriorly

(Aleev, 1963).   On the basis of these considerations it would seem probable that the more or less medially placed dorsal fins of such lower teleosts as *Elops*, *Chanos*, and *Salmo* serve primarily as keels.

With regard to these three genera, the first question that arises is whether the forward position of the dorsal fin is not a specialization among relatively large, active fishes?   Is it possible that this is one of the features made advantageous in some, perhaps all, of the early Teleostei by the reduction in scaly armour, the perfection of the externally symmetrical caudal fin (Patterson, 1968), etc.?

Second, if a median keel is advantageous only in relatively large, powerfully swimming fishes, then what do the small, weakly swimming larval and juvenile stages of these same fishes do with their dorsal fins?   Two rather different answers to this question have been provided by *Elops* and *Salmo*.

Elops has a long, transparent, ribbon-like " leptocephalous " larva, which undoubtedly swims by undulation of the body.   In this larva the dorsal and anal fins are placed far back, just ahead of the tail.   As the larval form grows and transforms into the adult, the dorsal (and anal) fins move forward on the body.   If the forward dorsal position of the adult *Elops* is a specialization, the extreme posterior position of the dorsal in the larva would also seem to be a specialization, but in the opposite direction.   Presumably the change in position is related to the different methods and requirements of swimming in the young and adult *Elops*.   In *Chanos* and the clupeoids (see, for example, Delsman, 1926, and François, 1956), forward movement of the dorsal fin during ontogeny also occurs, but to a lesser extent than in *Elops*.

Salmo lays large eggs, and the juveniles that hatch out have essentially the adult form.   The dorsal fin first appears in about its adult, forward position.   However, *Salmo* does have, behind the dorsal fin, a rayless adipose fin of problematic function (Wassnetzov, 1935; Kosswig, 1965).   Two questions come to mind.   One is whether the adipose fin of *Salmo* does not play the same role, whatever that is, of the more posteriorly placed dorsal fin of the juvenile herring, *Chanos*, etc.?   Second, could the adipose fin serve in some minor way to offset the otherwise asymmetrically placed anal fin below it?   The anal fin, acting as a rudder, might have two effects worth offsetting.   One is to twist the posterior end of the body and the other is to lift it.

Though they only bear peripherally on the alepocephaloid condition, a number of different groups have developed forms with a long anal fin which is presumably the principal locomotor organ, a tapering body, and a dorsal fin which, if present, is well forward.   Fishes of this type are the Gymnarchidae, *Coilia* among the Engraulidae, the Halosauridae, and certain catfishes.   Among these, the adipose fin tends to be lost among the catfishes, and the dorsal fin to be far forward in the larval halosaur (Mead, 1965).

Among alepocephaloids, *Bathylaco* is known to lay large eggs (Nielsen & Larsen, 1968) and *Bathytroctes* develops without any peculiar larval form or anterior movement of the dorsal fin with growth (Beebe, 1933).   This development would seem to be quite unlike that of elopoids, clupeoids and *Chanos*.   Further differentiation between alepocephaloids and *Elops* or clupeoids is the absence of a subtemporal fossa and any swimbladder to ear connection in alepocephaloids.

The possibility of a relationship between alepocephaloids and *Albula* seems no

greater, partly because of the larval specializations of *Albula* and its presumed derivatives, the eels and halosaurs, but also because of the lateral line peculiarities in the snout of these fishes (Allis, 1903; Gosline, 1961), etc.

Alepocephaloids have the dorsal fin well back on the body and no adipose fin. Other marine teleosts with this fin construction are *Gonorhynchus* and some stomiatoids. I can find no information on the ontogenetic development of *Gonorhynchus*, but it, along with other gonorhynchoids including *Chanos*, has a small mouth with peculiar jaw construction, a reduced number of branchiostegal rays, and one or more cephalic ribs (Greenwood, et al., 1966 : 375). Alepocephaloids show none of these specializations.

Those stomiatoid fishes with a posterior dorsal and no adipose form a highly specialized series of derivatives from forms with an adipose fin and the rayed dorsal farther forward. Though there would seem to be no direct relationship between alepocephaloids and stomiatoids (Weitzman, 1967a, b), the question could perhaps be raised of whether the stomiatoids and alepocephaloids are not two partially parallel endpoints in evolution from a single, if distant, stock. Weitzman (1967a) traces the stomiatoids back to an origin among a group of fishes rather like the present day osmerids. But neither the osmerids nor any of their present day relatives are sufficiently generalized, i.e., " primitive ", to have given rise to the alepocephaloids. None of them, for example, have the basipterygoid process or epibranchial organ found among alepocephaloids.

By a process of elimination, then, it appears that the alepocephaloids are perhaps least unlike the osmeroids among modern fishes. Characters held in common by the two groups are much too general in nature to more than suggest the possibility of such a relationship (Ridewood, 1904; Hennig, 1966). They include such features as the absence of forward movement of the dorsal fin during ontogeny, the absence of subtemporal fossae, and the presence of a single elongate uroneural (there are other shorter ones posteriorly) extending forward over the second pre-ural centrum in at least *Alepocephalus*, *Bathylaco* and salmonids. Some osmeroid derivatives have taken up a midwater oceanic existence alongside the alepocephaloids, and among these are forms which have adapted themselves to such an existence in certain alepocephaloid-like ways. This may indicate parallel development from a single basal stock and hence relationships of a distant sort; or, of course, it may be the result of convergent evolution from quite different basal stocks.

Defining the alepocephaloids is hardly less difficult than determining their relationships. Internal characters cannot be used because they are known in at best a few forms among a diverse group. Two skeletal features may be noted as holding promise in future definitions of the group. One is the long anterior uroneural in the caudal skeleton which occurs in *Alepocephalus* and *Bathylaco*. The other is the opercular series of bones. This series, though quite diverse in the species for which it is known (see, for example, Fig. 3) may prove to be peculiar in one way or another throughout the group. Meanwhile, the best that can apparently be done is to define the alepocephaloids in terms of general characteristics which in combination will serve to exclude other groups:

Oceanic, midwater, dark-coloured fishes with the maxillary included in the gape

and the dorsal fin over the posterior half of the body; without a swimbladder, adipose fin, enlarged fang-like teeth, or two long regular rows of small light organs along the lower sides.

ACKNOWLEDGMENTS

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